

THE RESPONSE OF *QUERCUS PALUSTRIS* TO ENVIRONMENTAL FACTORS

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ABSTRACT

The diurnal fluctuations in stem diameter and the daily radial growth of *Quercus palustris* growing in the Jonkershoek Forest Reserve were measured with microdendrographs. The data were correlated with meteorological records from an adjacent weather station.

Temperature and difference between precipitation and evapotranspiration appeared as the most influential variables. Independently of the effect of these factors the diurnal fluctuations continued to show short-term cycles within the annual cycle. This indicates that there is an internal control of shrinkage and swelling which is independent of the influence of external factors.

UITTREKSEL

DIE REAKSIE VAN *QUERCUS PALUSTRIS* OP OMGEWINGSFAKTORE

Die daaglikse wisseling in die deursnee van die stam asook die daaglikse groei van die *Quercus palustris* wat in die Jonkershoekbosreservaat groei, was deur middel van mikro-dendrograwe gemeet. Die data was gekorreleer met rekords van 'n naburige weerstasie.

Dit het voorgekom asof temperatuur en verskille tussen neerslag en evapotranspirasie die veranderlikes was wat die meeste invloed gehad het. Afgesien van die uitwerking van hierdie faktore het die daaglikse wisseling voortgegaan om kort kringlope binne die jaarlikse kringloop te toon.

Dit dui daarop dat daar 'n inwendige kontrole van die krimp en swelling is wat onafhanklik van die invloede van buite is.

INTRODUCTION

It is technically impossible to study the growth behaviour of mature trees under controlled conditions in greenhouses. A study of growth responses under natural conditions therefore may be useful to supplement experiments conducted with seedlings in controlled environments. Not only the influence of single factors, but also the interaction between several environmental factors may change with increasing age of the trees.

In several studies the site indices of stands have been correlated with observed external factors. In South Africa this method has been applied in plantations of black wattle (Schönau 1970). These studies can be useful to guide the forester in selecting species for specific sites, particularly in afforestation with exotics. The site index however, being an index of growth vigour, reflects the cumulative growth from the date of planting up to the present age of the stand but does not account for the year-to-year variations in certain environmental influences. In addition the site index of a stand is affected by management practices and by the

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occurrence of pests and diseases. Finally the method assumes that height growth is indicative for volume growth. Yield studies conducted in Germany however show that the relationship between height and total volume productions is influenced by undisclosed environmental factors, in addition to the widely recognized influence of stand density (Assmann 1961). It is apparent that diameter and height respond differently to the environment.

As an alternative to the site index method, the radial growth of mature trees can be measured over short periods within the growing season and correlated with environmental conditions prevailing during and prior to those periods. These studies afford a better understanding of the progressively changing influence of environmental factors on radial growth. The scope of these investigations is limited because the diameter growth during a given interval does not adequately reflect the total integrated effect of the physical environment.

This paper deals with a growth study conducted during the growing season 1968–1969 on two 25-year old trees of *Quercus palustris* in the Jonkershoek Forest Reserve in the south-western Cape Province. The author gratefully acknowledges permission granted by the Department of Forestry to conduct these studies and to use weather data from the Biesievlei meteorological station operated by the Department.

Quercus palustris is a species which grows under a wide range of conditions in the eastern and central states of North America, between 34° and 42° N latitude and between 70° and 96° W longitude. The mean annual temperature varies between 10° and 16°C and the rainfall between 900 and 1 300 mm per annum. The species grows in pure stands on heavy soils of excessive wetness, and in mixture with hardwoods on lighter and better-drained soils. The trees used in the present study were growing at an altitude of 700 ft/213,41 m above sea level at 33° 55' E longitude. Microdendrographs, providing a continuous record of the radial growth, were installed at breast height. The growth data were correlated with weather data from the nearest meteorological station Biesievlei, which is situated at an altitude of 950 ft/289,63 m above sea level and at a distance of 1,4 miles/2,25 km from the site of the experimental trees.

The rainfall from 1st April 1968 to 31st March 1969 was 1 438 mm, i.e. 6,1% above the 16-year average for this gauge, as calculated by Wicht (Wicht 1969). Of this total, 74,2% was recorded between April 1 and September 30. Of the summer rainfall, occurring between October 1 and March 31, 36,3% was recorded during October. November was the driest month, with a rainfall of 11 mm. The rain intensity, defined as the average precipitation on rainy days was 13,5 mm during the winter (April 1 to September 30) and 8,4 mm during the summer (October 1 to March 31). The average length of dry spells was 3,6 days

during the winter period and 6,7 days during the summer. During the winter period there were 14 and during the summer period 106 summer days with a maximum temperature $> 25^{\circ}\text{C}$. The number of tropical days with a maximum temperature $> 30^{\circ}\text{C}$ was 1 during winter and 35 during the summer.

The daily maximum and minimum temperatures were linearly related. An analysis of covariance indicated that the slopes of the regression lines for the previously defined summer- and winter periods did not differ significantly but the difference between the levels was significant at 0,01. The equations were:

$$\text{summer period: } T_{\min.} (^{\circ}\text{C}) = 4,58 + 0,308 T_{\max.} (^{\circ}\text{C})$$

$$\text{winter period: } T_{\min.} (^{\circ}\text{C}) = 1,66 + 0,308 T_{\max.} (^{\circ}\text{C})$$

For a 1° increase in the daily maximum temperature the daily minimum temperature increases by $0,31^{\circ}\text{C}$. At a given maximum temperature the minimum temperature during the summer period was 3° higher than during the winter period. For the summer period the variance about the regression line was $7,41^{\circ}$ and for the winter period this variance was $12,32^{\circ}$. This indicates that the variation around the regression line during the winter was significantly greater than during the summer ($F = 1,66$, 181 and 180 degrees of freedom). For a daily maximum temperature of 25°C , the minimum temperature was $12,28^{\circ}\text{C}$ during the summer period and $9,36^{\circ}\text{C}$ during the winter period. For a confidence coefficient of 0,95 the confidence interval for a single predicted minimum temperature for $T_{\max.} = 25^{\circ}$ was $12,28 \pm 2,73^{\circ}$ during the summer and $9,36 \pm 3,53^{\circ}$ during the winter.

On rainy days during the winter period, temperature and rainfall were significantly related ($r = 0,374$, 77 degrees of freedom). The regression equation was:

$$T_{\text{mean}} (^{\circ}\text{C}) = 12,308 - 0,0262 (\text{rainfall in mm})$$

On rainless days during this period, the mean daily temperature was $13,43^{\circ}\text{C}$. During the summer period the mean temperature and rainfall on rainy days were not related ($r = 0,241$, 42 degrees of freedom). On rainy days the average mean daily temperature was $16,21^{\circ}\text{C}$ and on rainless days $19,74^{\circ}\text{C}$. The difference between these means was highly significant ($t = 5,95$, 178 degrees of freedom).

During the winter period there was a highly significant correlation between hours sunshine and rainfall on rainy days ($r = 0,374$, 77 degrees of freedom), the regression equation being as follows:

Hours sunshine: $2,855 - 0,0526 (\text{rainfall in mm.})$ On rainless days during this period the average number of hours sunshine was 6,6. During the summer the correlation between hours sunshine and rainfall on rainy days was not

significant ($r = 0,168$, 42 degrees of freedom.) The average number of hours sunshine was 4,43 on rainy days and 8,9 on rainless days.

PROCEDURE AND RESULTS

Microdendrographs, providing a continuous record of radial dimensional changes in the diameter of tree trunks were installed on two mature trees of *Q. palustris* at Jonkershoek, at a height of 4,5 ft/1,37 m above ground. The instruments were equipped with 7-day clocks and provided a 1:100 magnification of radial swelling and shrinkage. Daily fluctuation and daily growth, measured on the dendrograph charts were correlated with meteorological data of Biesievlei.

(1) Diurnal fluctuations.

Previous studies, conducted in *Pinus radiata* and *Populus deltoides* revealed the occurrence of diurnal fluctuations in the diameter of tree trunks (van Laar 1967, 1969). Fluctuations occurring in the xylem and phloem result from absorption lagging behind transpiration, whereas swelling and shrinkage of the bark can be described as a physical evaporation and dehydration process.

During day-time, the rate of transpiration exceeds the rate of water absorption but during the night the position is reversed. For this reason the stem diameter reaches a daily maximum at about 8.00 a.m. and a minimum at 5.00 p.m. For the purpose of this study the daily fluctuation was expressed as the average of the differences between the early-morning maximum and late-afternoon minimum and that between this minimum and the maximum on the next morning. This is an adequate expression for the diurnal fluctuation, although it should be borne in mind that a shower occurring after the afternoon minimum but before 8.00 a.m. on the next day will increase the calculated fluctuation. The readings started on 4th October and were discontinued on 22nd May. After this date no noticeable fluctuations were observed. The annual course of the daily fluctuations, represented as moving averages for 7-day periods is shown in fig. 1. There is a pronounced annual trend which, for the first part of the growing season coincides with the annual growth curve. Within this annual cycle there are clearly distinguishable oscillations of varying lengths. A run-test in which the single observations were classified as above or below the trend, indicated rejection of the hypothesis of randomness at a risk level far below 0,01.

The serial correlation, defined as the correlation between pairs of values of a time series with a fixed distance apart, has been calculated for lags up to 7 days.

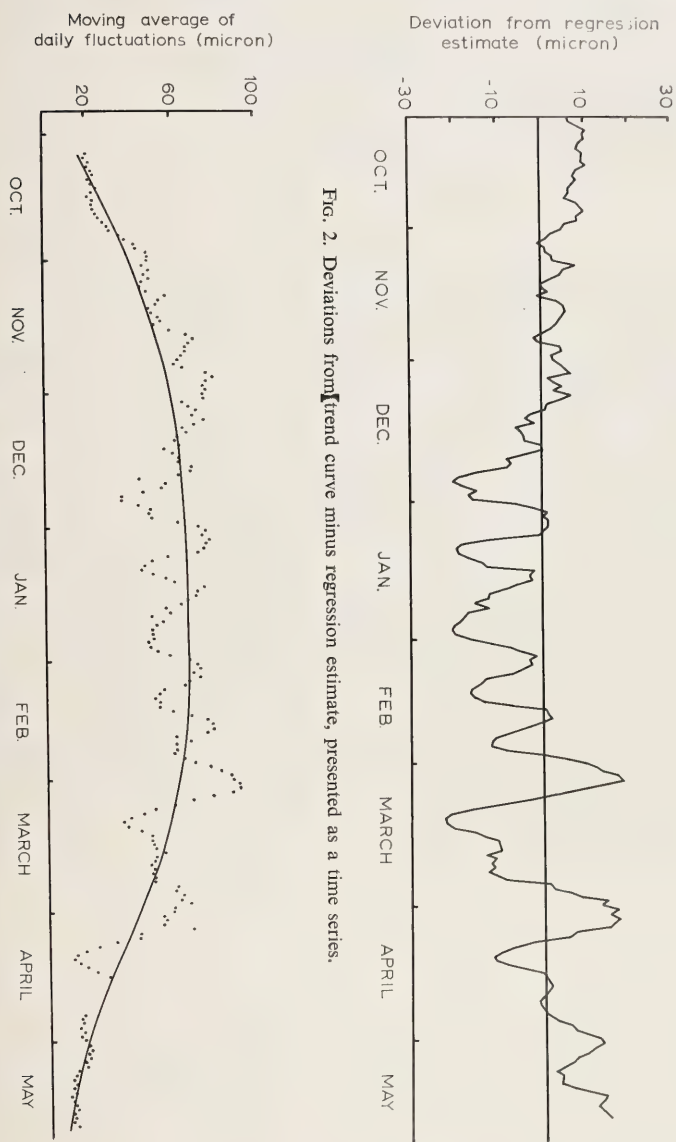


Fig. 2. Deviations from trend curve minus regression estimate, presented as a time series.

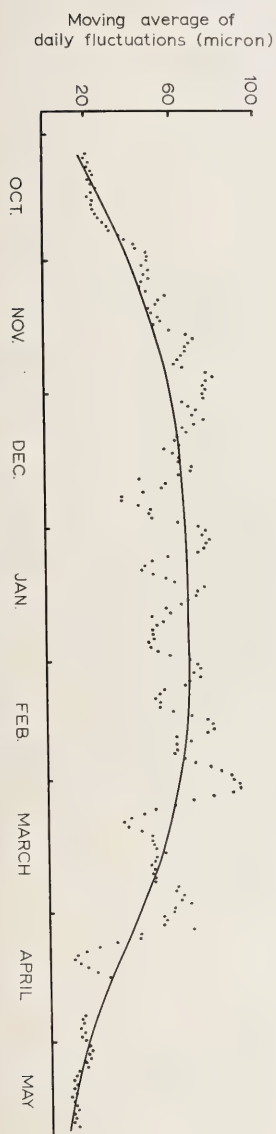


Fig. 1. Moving average of dark fluctuations.

The results are given below:

Lag (days)	serial correlation
1	+ 0,344
2	+ 0,230
3	+ 0,051
4	+ 0,028
5	— 0,102
6	— 0,117
7	— 0,122

The correlation coefficient decreased with increasing interval between the items of the series. The correlation was significantly positive for lags of 1 and 2 days. Hence, a positive deviation from the trend is likely to be followed by a positive deviation during the next 2 days. The algebraic value of the correlation coefficient decreased with increasing lag, but the lowest absolute value was found for a 4-day distance. For a time lag of more than 4 days, the correlation was negative, although non-significant. A level of significance of 0,08 was observed for a lag of 7 days. This indicates that a positive deviation on a given day is likely to be followed by a negative deviation 7 days later. It demonstrates the occurrence of short-term oscillations within the annual cycle. It is also of interest to note that these cyclical variations were most pronounced during the summer months. This must be explained in terms of the more critical water supply during this period. A dry spell during summer will have an immediate and prolonged effect on the internal water balance of the tree and consequently on the magnitude of the diurnal fluctuations. During spring and autumn the soil moisture content is higher, the rate of evapotranspiration lower and the internal water balance more favourable than during summer.

For a study of the influence of external factors, the fluctuations were expressed as a deviation from the trend. This eliminated the necessity to incorporate time as an independent variable. The following variables were introduced into the regression equation:

maximum temperature on the day of measurement ($T_{\max}$) average maximum temperature during the preceding 5 days ($T_{\max(5)}$)

precipitation minus Thornthwaite's evapotranspiration on the day of measurement (P-PET)

precipitation minus evapotranspiration, average value over the last 5 days (P-PET(5)),

all linear interactions between these variables.

The contribution of these variables was tested in a stepwise multiple regression analysis. $T_{\max}$, $T_{\max(5)}$, (P-PET), (P-PET(5)) and the interaction between $T_{\max(5)}$ and (P-PET(5)) were significantly related with the dependent variable.

The index of multiple determination was 0.545. Unlike earlier studies in *P. radiata*, the results of the regression analysis were not readily interpretable. The regression coefficient for Tmax was positive but those for Tmax(5) and for the interaction between Tmax(5) and (P-PET(5)) were negative. Although there is no doubt about the statistical significance of these variables it is unlikely to reveal a causal relationship. For this reason, some variables were dropped and Tmax and (P-PET) retained in the final equation. The result was as follows:

Diurnal fluctuation (deviation from trend, in micron) =

$$- 64,4596 + 2,6562 (\text{Tmax}) + 0,7649 (\text{P-PET}).$$

Temperature is the most influential factor amongst those tested in the regression analysis. With an increase in temperature, the moisture stresses in the tree become greater and the amplitude of the daily cycle increases. The regression coefficient for (P-PET) was positive. This does not necessarily contradict our previous conclusions but is associated with the method of determining the diurnal fluctuation. If during a given day rain occurs after the lowest value of the diameter has been reached, the immediate dehydration and swelling will increase the magnitude of the daily fluctuations measured on the charts. Most frequently the difference between precipitation and water losses will then be positive, partly because the lower temperature on rainy days reduces the rate of evapotranspiration.

For each day during the growing season the difference between the deviation from the trend curve and the regression estimate of this deviation was calculated and presented as a time series (fig. 2).

The average difference must necessarily be equal to zero, because the regression estimates of the deviations were calculated with the method of the least squares. It can be expected that the single values of the time series show randomness, if the regression analyses has been successful to disclose causal relationships. Fig. 2 however indicates that these differences exhibit a time-related trend. During spring, early summer and autumn they tend to be positive and during mid-summer negative. In addition, cyclical variations are retained, indicating that the relationships are more complex and that internal moisture stresses, inducing diurnal fluctuations, cannot be ascribed to environmental influences only.

(2) *Daily growth.*

The period of diameter growth extended from the beginning of October until mid-February and was recorded between 1st October and 19th February. After this date, the trees continued to produce fluctuations but the process of active growth was discontinued. The daily growth was measured as the difference between a chart reading at 8.00 a.m. and 8.00 a.m. on the following day.

Similarly to the analysis of the diurnal fluctuations, 7-day moving averages were calculated and smoothed graphically. The growth record on a given day was expressed as a deviation from this trend curve.

In the regression analysis the daily growth was correlated with:

mean temperature on the day of measurement

mean temperature on the previous day

(P-PET) on the day of measurement and that on the previous day

all linear interactions between these variables.

Tested at the 0,01 level of significance, the analysis of variance was as follows:

Source of variation	degrees of freedom	sum of squares	F
X_3	1	19110,58	31,2
X_9	1	11137,00	18,2
X_8	1	4865,12	7,9
residuals	138	84588,69	—

The resulting equation was:

$$Y = -52,889 + 2,87718 X_3 + 0,09673 X_9 - 0,07625 X_8$$

where: X_3 = mean temperature ($^{\circ}\text{C}$) on the previous day

X_9 = (mean temperature on the previous day) $\times$
(P-PET on the day of measurement)

X_8 = (mean temperature on day of measurement) $\times$
(P-PET on previous day)

Y = growth in micron (deviation from trend).

The index of multiple determination was 0,293. The regression coefficients for X_3 and X_9 were positive. In the regression analysis, X_3 , the mean temperature on the preceding day appeared to be the most influential environmental factor. In addition a combination of a high temperature on the previous day and a moisture surplus on the current day was positively related to growth. The variable X_8 , which expresses the influence of the interaction between mean temperature on the day of measurement and (P-PET) on the previous day and evaluates the relationship independently of those existing between Y and X_3 , and X_9 respectively, was negatively related to growth. It is difficult to interpret this negative regression. Possibly, the difference between precipitation and water losses by vaporization, calculated with Thornthwaite's method does not satisfactorily express the water balance of the tree. A combination of a high temperature on the day of measurement and a moisture surplus on the previous day might eventually be inhibiting for growth, because of soil moisture depletion, associated with periods of high temperature.

The approach in the present study has certain short-comings. Instead of calculating the difference between precipitation and atmospheric water losses, it might be more useful to obtain a continuous record of the fluctuations of the soil moisture content. In addition, it has been found that the multiple regression analysis may give results, which are difficult to interpret. Growth is a highly complex phenomenon, which is causally influenced by the physical environment of the tree, but also by other, internal factors, which in turn may be related to environmental factors, ignored in the growth study.

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